

# Fan Organs of Crayfish Enhance Chemical Information Flow

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**Abstract.** Animals as well as autonomous robots need to acquire environmental signals in order to adjust their activity in time and space. Some information is accessible to the sensors only as a result of specific behaviors for stimulus acquisition. Due to the slow rate of molecular diffusion, dispersal of chemical stimuli depends on fluid flow. Aquatic crustaceans can generate directed water currents by specialized appendages. Here I describe the crayfish fan organs, which are feathered flagella of the mouthparts, and their activity in sending and receiving chemical signals in environments with stagnant flow conditions. During the power-stroke, the fan opens and displaces water; during the return stroke, it collapses and thereby minimizes drag. These organs can create a variety of flow fields including water jets, and in many different directions. Bilateral upward fanning draws water horizontally from all directions toward the anterior chemoreceptors. Unilateral upward fanning draws water from only one side towards the body. The versatility of the crayfish fan organ makes it a candidate for biomimetic reconstruction and use in autonomous robots that can search chemical sources.

## Exchange of Chemical Information at Different Size Scales

A prerequisite of life is the exchange of matter and information between an organism and its environment. Whereas the exchange of (organic) matter is necessary for

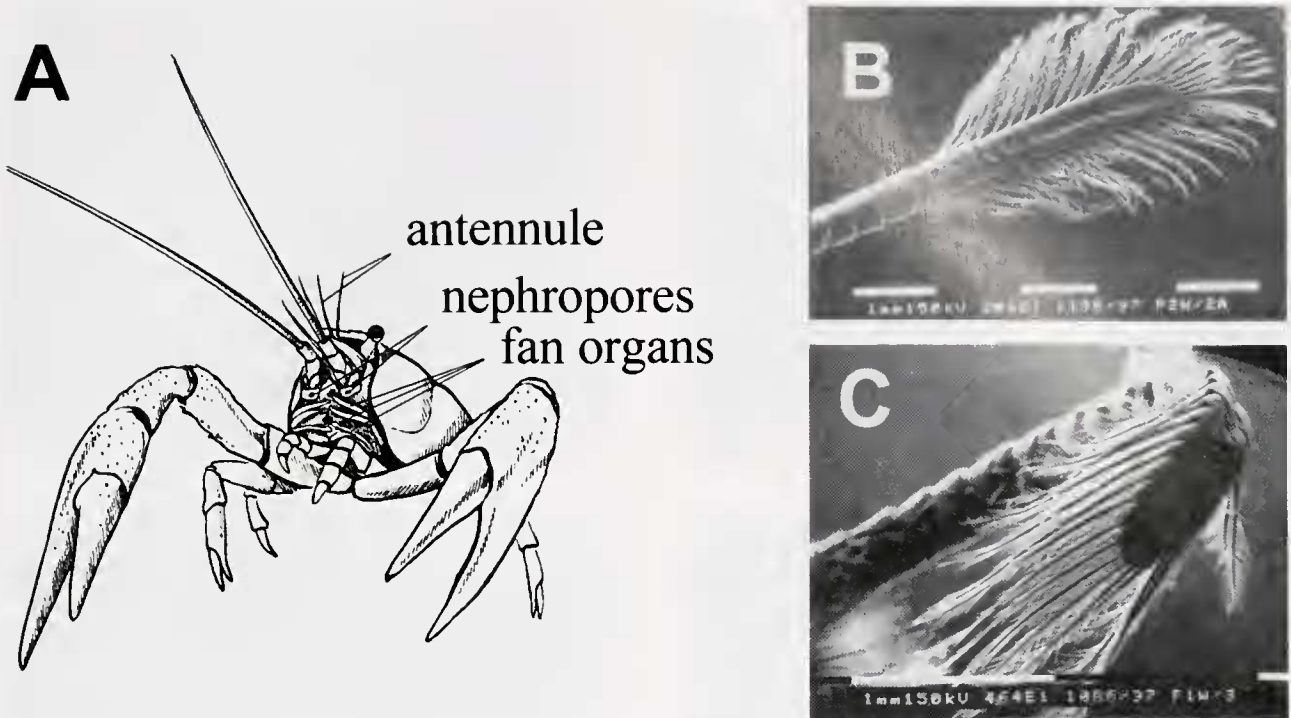
nutrient uptake by and waste removal from living organisms, the acquisition of information that serves to modify the behavior of organisms with respect to environmental resources (*e.g.*, water, food, mates) and threats (*e.g.*, predators, obstacles) is important for any living organism as well as for autonomous robots.

The oldest method of information exchange is by means of chemical stimuli. Microorganisms (*e.g.*, motile bacteria) need to search for micropatches of higher nutrient concentration and adjust their motility with respect to chemical stimuli (Blackburn *et al.*, 1998). Microorganisms also exchange chemical signals ("pheromones") with conspecifics to synchronize their mating activity (Agosta, 1992). The movement of chemicals from a source to a receiver at such small size scales (below 0.1 mm, Reynolds number below  $10^{-2}$ ) is driven by molecular diffusion, or random molecular motion. Cohesion among water molecules at that scale makes it almost impossible to influence the direction of chemical information flow except by locomotion of the whole organism.

With increasing size and velocity of organisms (increasing Reynolds number) molecular diffusion loses in importance for the dispersal of chemicals (Weissburg, 2000). In water, molecular diffusion is a very slow process that on average would displace a molecule by no more than 0.7 mm (70 mm in air) in 1 min and by only 5 mm (500 mm in air) in 1 h (Dusenbery, 1992). Water flow is much more effective in dispersing odor molecules, and animals can influence the flow in their immediate neighborhood by using undulating, beating, or fanning appendages. By modulating the nearby flow pattern, they can facilitate the exchange of chemical information with their environment. Insects as well as some vertebrates use wing-fanning for delivering pheromones to their mates (bees: Free, 1987; butterflies: Boppré, 1984; bats: Voigt and von Helversen, 1999). Wing-fanning may facilitate odor perception by drawing nearby

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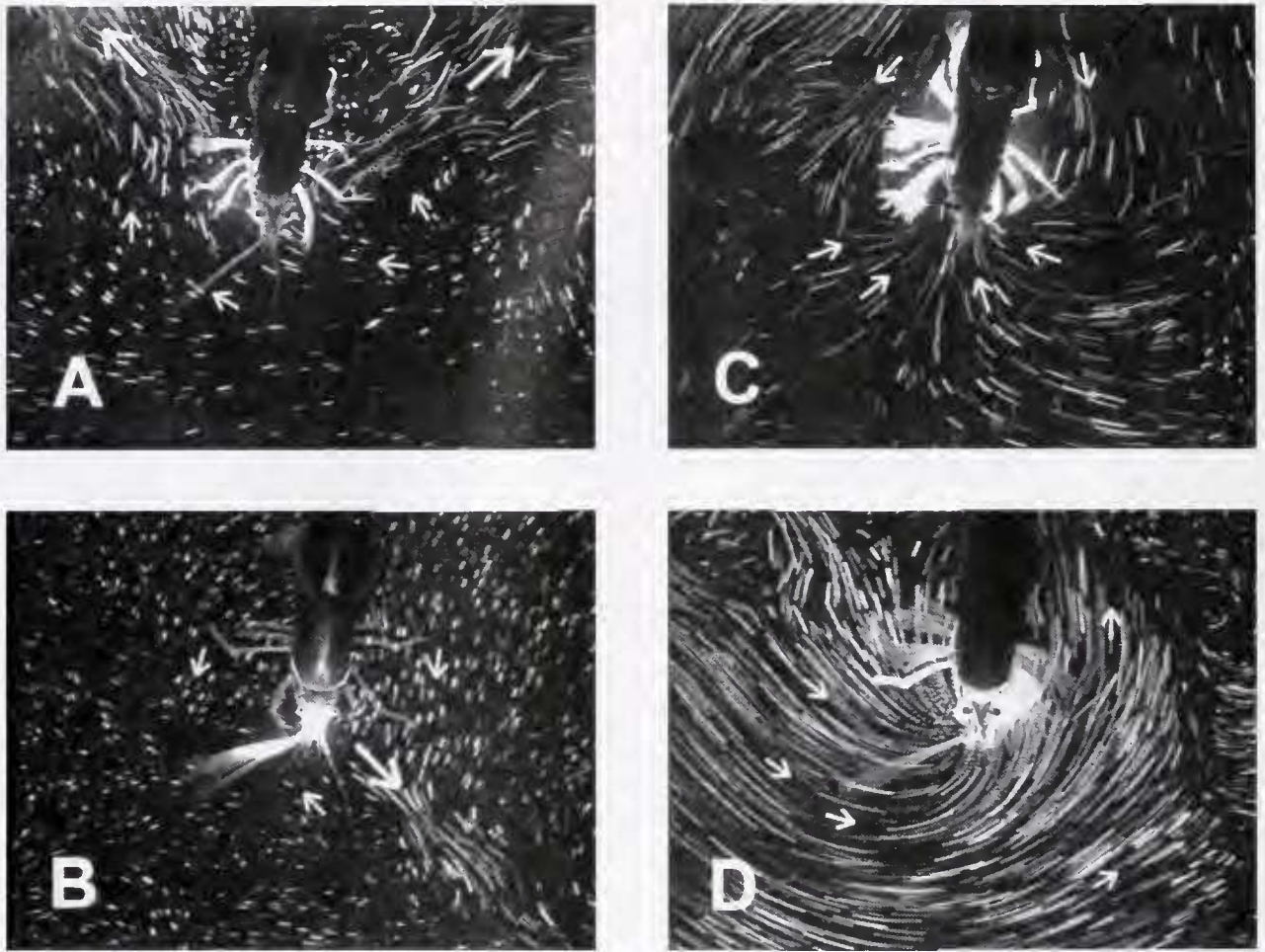
**Figure 1.** (A) Location of fan organs, urinary pores (nephropores), and major chemoreceptor organs (antennules) of crayfish. (B) The fan organs are multi-segmental flagella of the mouthparts (maxillipeds) with feathered setae on the distal part. During the power stroke (scanning electron microscopy "SEM" picture of *Procambarus clarkii*) the feathered hairs are extended. (C) During the recovery stroke (SEM picture of *Procambarus clarkii*) the feathered hairs are tilted downstream. White scale bars in SEM pictures represent 1 mm.

molecules towards the receptors. Wing-fanning of silkworm moths in response to pheromone (Agosta, 1992) may aid in stimulus acquisition (Ishida *et al.*, 1996). Crustaceans are well known for their ability to create directed water currents by pumping or fanning appendages (Brock, 1926; Burrows and Willows, 1969; Budd *et al.*, 1979; Koehl and Strickler, 1981; Atema, 1985; Lavalli and Factor, 1995). This behavior can be used for gill ventilation, locomotion, suspension feeding, and chemoreception or chemical signaling. Planktonic copepods, small crustaceans of 1 to 10 mm, generate water currents that are used for capturing food particles and that carry odor information from the food particles to the chemoreceptors (Yen, 2000). Here I describe the fanning behavior of crayfish, typical of larger crustaceans, that is used for both sending and receiving chemical signals in aquatic environments with stagnant flow conditions.

#### Maxilliped Flagella, the Fan Organs of Crayfish

One of the first reactions of many crustaceans to chemical stimulation is the onset of the rhythmic beating of three pairs of flagella of the maxillipeds (mouthparts). These so-called fan organs (Atema, 1985) in crayfish are distrib-

uted around the mouth opening below the major chemoreceptor organs ("antennules") and the urinary pore ("nephropore") (Fig. 1A). Each fan organ consists of a multi-segmental, flattened stem. It is feathered in one plane, with setae emerging laterally on both sides of the flattened stem (Fig. 1B). The setae are feathered themselves, and their rami overlap with those of adjacent setae to form a dense layer (Fig. 1B). During the power stroke, the fan—with stem erect and setae extended—acts like a paddle propelling fluid past the organism (Fig. 1B; Cheer and Koehl, 1987). During the recovery stroke, the setae are tilted downstream and the stem is flexed (Fig. 1C). This behavior reduces the area of the leading, water-displacing surface and therefore effectively reduces the drag during the return stroke. This fanning activity is similar to that of a rowing paddle and can generate unidirectional flow. All three flagella on one side usually beat simultaneously and with the same frequency (between 5 and 8 Hz in *Procambarus clarkii*). The rhythmic movements of the three flagella are metachronally phase-shifted by about 0.2 to 0.5 wavelengths (data from high-speed video-recordings; Breithaupt, unpubl. data). By changing the angle of the mouthparts, the flagella can modify the axis of fanning activity. By fanning only one side or



**Figure 2.** Examples of horizontal flow fields generated by the fan organs of an adult male crayfish (*Procambarus clarkii*) without claws. Flow pictures were generated by superimposing 25 video-frames (Breithaupt and Ayers, 1998) of neutrally buoyant particles moving in a 5-mm-thick horizontal light sheet, and tracing the flow lines. (A) Fans of both sides beat backward and generate bilateral backward-directed water jets (light sheet at 1 cm above ground lasting for 2 s). Large arrows indicate fluid velocities of 1 cm/s; small arrows represent velocities of 0.5 cm/s. (B) Fans of left side only are beating forward and produce a forward-directed jet (at 3.5 cm for 2 s; arrows as in A). (C) Fans of both sides beat upward and in the horizontal plane draw water from all directions towards the frontal mouthparts (at 1 cm for 10 s). Arrows denote fluid velocities of 0.1 cm/s. (D) Fans of right side only beat upward and draw water from right to left (at 2.5 cm for 12 s; arrows as in C).

both sides and by changing the direction of fanning activity, crayfish can generate a variety of flow fields.

#### Flow Fields Generated by the Fan Organs

Visualization of the flow fields using small ( $50\ \mu\text{m}$ ), neutrally buoyant particles illuminated within a horizontal and a vertical light sheet (Breithaupt and Ayers, 1998) revealed that crayfish can modulate the flow environment in their immediate vicinity in a variety of ways (Fig. 2). In the horizontal plane that is probably most significant for most of the crayfish's activities, the flow can be directed either away from (Fig. 2A, B) or toward (Fig. 2C, D) the head region.

Flow velocity of the outgoing water jets can be up to 4 cm/s. Incoming water in the horizontal plane is usually much slower, with velocities between 0.1 and 0.5 cm/s depending on the distance to the fan organs. By beating the flagella on only one side, crayfish can draw in water exclusively from this side (Fig. 2D).

#### Biological Significance of Fanning Behavior

Many crayfish species live in environments with stagnant flow conditions. The flow velocity in a lake inhabited by the European narrow-clawed crayfish (*Astacus leptodactylus*) rarely exceeds 1 cm/s even on stormy days (T. Breithaupt

and E. Ebert, unpubl. data). In such environments, flow fields created by the animals themselves help in getting access to distant odor stimuli and provide directional information. Fanning is a major activity of crayfish during food search in stagnant water. Blindfolded crayfish (*Astacus leptodactylus*) with restrained fan organs that could not generate water currents were not able to find the odor source (T. Breithaupt and E. Ebert, unpubl. data). This demonstrates the importance of the fan organs in actively scanning the environment and transporting the odor molecules towards the chemoreceptors on the antennules (Fig. 1). The crayfish may identify the direction of the odor source by comparing the arrival time of the moving odor patches at different receptor locations on the bilateral antennules. Recent studies suggested bilateral directional information as a critical element in chemical orientation of decapod crustaceans at turbulent flow conditions (Atema, 1996; Grasso *et al.*, 1998).

A second important function of the fan organs is to carry urine-borne pheromone from the nephropores to the chemoreceptors of nearby conspecifics. Visualization of urine release during fights of American lobsters and crayfish revealed that signaling with urine is an integral component of aggressive communication in these animals (Breithaupt and Atema, 2000; T. Breithaupt and P. Rohleder, unpubl. data). The crayfish *Procambarus clarkii* uses frontally projecting fan organ currents to carry urine signals toward the opponent (T. Breithaupt and P. Rohleder, unpubl. data). The currents are also used to direct urine signals in directions other than forward.

### Lessons to Learn From the Fan Organs of Crayfish

Only by using such elaborate appendages can crustaceans acquire and send chemical information in environments with stagnant flow conditions. Fan organs are widely used in the animal kingdom to propel and direct chemical stimuli away from and toward organisms. Flow-generating devices can also greatly enhance the search success of autonomous robots orienting to chemical sources. The use of a rotating propeller fan has been shown to help terrestrial autonomous robots to locate chemical sources by actively drawing air to their chemical sensor and scanning different directions for the presence of chemicals (Nakamoto *et al.*, 1999; Ishida *et al.*, 2001). Recent progress in the development of aquatic robots has been inspired by research on crustaceans (Grasso, 2001). The versatility of the paddlelike fan design of the crayfish appendage goes beyond that of propeller fans by enabling the exchange of chemical information in three dimensions. A thorough analysis of the behavior and the mechanics of flow production as well as the underlying muscular and neural activity should further illuminate the

functional organization of this beautiful system and may trigger biomimetic designs for artificial fans.

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